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How intelligent is a cephalopod? Lessons from comparative cognition

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ABSTRACT

The soft-bodied cephalopods including octopus, cuttlefish, and squid are broadly considered to be the most cognitively advanced group of invertebrates. Previous research has demonstrated that these large-brained molluscs possess a suite of cognitive attributes that are comparable to those found in some vertebrates, including highly developed perception, learning, and memory abilities. Cephalopods are also renowned for performing sophisticated feats of flexible behaviour, which have led to claims of complex cognition such as causal reasoning, future planning, and mental attribution. Hypotheses to explain why complex cognition might have emerged in cephalopods suggest that a combination of predation, foraging, and competitive pressures are likely to have driven cognitive complexity in this group of animals. Currently, it is difficult to gauge the extent to which cephalopod behaviours are underpinned by complex cognition because many of the recent claims are largely based on anecdotal evidence. In this review, we provide a general overview of cephalopod cognition with a particular focus on the cognitive attributes that are thought to be prerequisites for more complex cognitive abilities. We then discuss different types of behavioural flexibility exhibited by cephalopods and, using examples from other taxa, highlight that behavioural flexibility could be explained by putatively simpler mechanisms. Consequently, behavioural flexibility should not be used as evidence of complex cognition. Fortunately, the field of comparative cognition centres on designing methods to pinpoint the underlying mechanisms that drive behaviours. To illustrate the utility of the methods developed in comparative cognition research, we provide a series of experimental designs aimed at distinguishing between complex cognition and simpler alternative explanations. Finally, we discuss the advantages of using cephalopods to develop a more comprehensive reconstruction of cognitive evolution.

Key words: octopus, cuttlefish, squid, cognitive mechanisms, complex cognition, cognitive evolution, convergent evolution

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I. INTRODUCTION

The study of complex cognition was traditionally confined to primates because they were considered to be the pinnacle of cognitive complexity (for a glossary of terms used herein, see Table 1). Over the past 20 years, however, there has been increasing evidence to suggest that distantly related large-brained vertebrates, from cetaceans (Marino, 2002; Fox, Muthukrishna, & Shultz, 2017) and elephants (Plotnik, de Waal, & Reiss, 2006; Plotnik *et al.*, 2011) to parrots (Pepperberg, 2006; Pepperberg *et al.*, 2013) and corvids (Emery & Clayton, 2004; Clayton, Dally, & Emery, 2007; Boeckle & Bugnyar, 2012), are capable of cognitive feats comparable to those found in primates (Table 2). In particular, the discovery that corvids possess complex abilities that match or exceed those exhibited by apes has prompted important questions about the evolution of complex cognition. Despite diverging approximately 300 million years ago, both apes and corvids demonstrate comparable cognitive sophistication (Emery & Clayton, 2005; Güntürkün & Bugnyar, 2016), which suggests that complex cognition evolved multiple times, independently (Roth, 2015). Two different evolutionary processes have been proposed to explain independently evolved yet similar traits. Comparable evolutionary pressures can trigger the emergence of similar traits either from the same underlying mechanisms through parallel evolution or from different underlying mechanisms through convergent evolution (Osvath, Kabadayi, & Jacobs, 2014). Given the dramatic differences in brain anatomy and neuroarchitecture between apes and corvids (Jarvis *et al.*, 2005), it is unlikely that their cognitive similarities have arisen from the same underlying mechanisms. For example, the mammalian neocortex, involved in complex cognitive abilities, is laminated whereby the cells are organised into layers, whereas the analogous brain structure in birds (i.e. the avian pallium) is nucleated, whereby the cells are organised into clusters. Such differences at the mechanistic level suggest that cognitive traits in corvids that resemble those found in apes are likely a result of convergent evolution arising independently in response to similar evolutionary pressures (Emery & Clayton, 2004; Seed, Emery, & Clayton, 2009b).

Moving beyond vertebrates, new findings amongst invertebrates provides further evidence that intelligence has evolved independently multiple times. A substantial amount of this evidence is emerging from one major group of invertebrates, the coleoid cephalopods, which diverged radically from vertebrates over 550 million years ago (Fig. 1). The coleoid cephalopods (henceforth cephalopods), which include octopus, cuttlefish, and squid have the most centralised and largest nervous system of all invertebrates, with a brain to body size ratio greater than most fish and reptiles (Packard, 1972; Nixon & Young, 2003). Such findings are intriguing given that many of the molluscan relatives of cephalopods, including gastropods and bivalves, have rudimentary nervous systems (Nixon & Young, 2003; Zullo & Hochner, 2011). Cephalopods also possess a suite of cognitive attributes that are comparable to those found in some vertebrates, including highly developed perception (Wells, 1978; Abbott, Williamson, & Maddock, 1995; Budelmann, 1995; Yang & Chiao, 2016; Hanlon & Messenger, 2018), learning (Fiorito & Scotto, 1992; Boal, 1996; Darmaillacq *et al.*, 2004; Cole & Adamo, 2005; Agin *et al.*, 2006*a*; Darmaillacq, Dickel, & Mather, 2014; Billard *et al.*, 2020b) and memory abilities (Sanders, 1975; reviewed in Agin *et al.*, 2006b; Jozet-Alves *et al.*, 2013). While these mechanisms are not among those most often used as evidence of complex cognition (Emery & Clayton, 2004), many of them are considered to be vital precursors for complex cognitive abilities such as causal reasoning, imagination, mental time travel, and mental attribution (Table 1). Although such complex abilities have primarily been demonstrated in large-brained vertebrates, some cephalopods have been reported performing sophisticated feats of flexible behaviour that have led to postulations of complex cognition (reviewed in Mather & Dickel, 2017; Amodio *et al.*, 2019a, 2019b). For example, veined octopuses, *Amphioctopus marginatus*, have been observed carrying coconut shells around as mobile dens, a behaviour that is thought to decrease the likelihood of predation as the coconut shells can be arranged into a protective encasing (Finn, Tregenza, & Norman, 2009) (Fig. 2). This has led to claims of future planning suggesting that octopuses can envisage that the coconut shells will protect them from predators that they may encounter in the future (Mather & Dickel, 2017; Mather, 2019).

The prospect that complex cognition emerged in cephalopods challenges a fundamental aspect of our current understanding of cognitive evolution. Presently, it is thought that environmental and social complexity has played key roles in the evolution of complex cognition, driving the emergence of flexible adaptive behaviour (i.e. behavioural flexibility). Consequently, the leading hypotheses suggest that complex cognition in large-brained vertebrates evolved under two key pressures. The first, the Ecological Intelligence Hypothesis, suggests that complex cognition emerged due to the physical demands of the environment, such as locating and processing food as well as memorising when it would be optimal to eat (i.e. fresh or ripe) (Milton, 1981; Gibson, 1986; Rosati, 2017). The second, the Social Intelligence Hypothesis, posits that complex cognition evolved to meet the challenges of living in a complex social group, such as the need to outwit group members through manipulation or

Table 1. Glossary of terms

Term	Definition
Associative learning	A process where an individual learns the relationship between two cues; or a cue and a behavioural response.
Behavioural flexibility	The ability innovatively to modify behaviour to respond effectively to novel situations.
Causal reasoning	The process of identifying the relationship between a cause and its effect.
Complex cognition	The collection of complex cognitive abilities including causal reasoning, imagination, mental time travel, and mental attribution.
Conditioning	Learning to respond to new stimuli using old behaviours.
Episodic-like memory	The ability to re-experience specific past events based on what happened, where it happened, and when.
Future planning	The ability to plan for future contingencies to fulfil future needs. Planning must be spontaneous without relying on learnt patterns and individuals must distinguish current motivational states from future states.
Hardwired predisposition	Fixed action patterns triggered by a cue.
Imagination	A process by which scenarios and situations that are not currently available to perception are formed in the mind's eye to facilitate innovative problem-solving.
Inferential reasoning	The ability to select the correct alternative by logically excluding other potential alternatives.
Intelligence	A suite of complex cognitive abilities including causal reasoning, imagination, mental time travel, and mental attribution. In this review, this term is used interchangeably with complex cognition.
Mental attribution	The ability to attribute the perceptual or attentional mental state of another individual, recognising others as individuals with their own thoughts, knowledge, and desires different from their own (also termed Theory of Mind).
Mental time travel	The ability to travel backwards and forwards in the mind's eye, to remember the past (i.e. episodic memory) and plan for the future.
Metacognition	The awareness and understanding of one's own thought processes.
Self-control	The ability to delay gratification by resisting the temptation of an immediate reward in preference for a better but delayed reward.
Self-recognition	The ability to recognise oneself as an individual separate from the environment and other individuals.

deception as a means of achieving higher social success and monopolising more resources including food, shelter, and mates (i.e. Machiavellian intelligence) (Jolly, 1966; Humphrey, 1976; Byrne & Whiten, 1988). Moreover, individuals that live in complex social groups also need to form and maintain social bonds (Dunbar, 1998), which has facilitated the emergence of cooperative behaviours such as group hunting, group defence, cooperative breeding, and pro-social helping.

The prospect of complex intelligence arising in cephalopods presents a challenge to this latter hypothesis because, compared to large-brained vertebrates, many species evolved in relatively simple social environments. For example, recognition abilities of cephalopods are rather primitive (Boal, 2006), there is no evidence of parental care, and embryos tend to disperse after hatching (Hanlon & Messenger, 2018). These life-history characteristics limit the opportunity for social interactions between kin, as well as the opportunity for forming strong social bonds, and restricts their ability to foster cooperative behaviours (Schnell & Clayton, 2019). It has recently been suggested that partially different evolutionary pressures are likely to have played a role in the evolution of cephalopod cognition (Amodio *et al.*, 2019a, 2019b). The immediate ancestors of cephalopods relied on an external shell for protection as well as for movement (i.e. the shell functioned as a buoyancy device). The loss of this structure was followed by dispersed colonisation of diverse ecological niches ranging from tropical to polar habitats, exposing soft-bodied cephalopods to a novel array of foraging and predatory challenges. Soft-bodied cephalopods are also faced with intense mating pressures. Most species are short-lived (lifespans typically shorter than two years) and have a single reproductive period in which eggs are laid in a single or several temporally finite instances (Rocha, Guerra, & González, 2001; Hanlon & Messenger, 2018). A combination of limited breeding periods, occasional post-mating cannibalism, and a highly skewed operational sex ratio experienced by various species results in fierce mating competition (Moynihan & Rodaniche, 1982; Hanlon *et al.*, 2005: Hanlon & Forsythe, 2008; Morse & Huffard, 2019). These three pressures – increased predation, increased foraging challenges, and intense mating competition – are thought to have driven the behavioural flexibility observed in cephalopods (Hanlon & Messenger, 2018; Schnell & Clayton, 2019; Amodio *et al.*, 2019a, 2019b).

Behavioural flexibility is widely considered to be the gold standard for evidence of complex cognition because it is thought that flexible behaviours are underpinned by complex cognitive abilities such as causal reasoning, imagination, mental time travel, and mental attribution. Despite this implicit assumption, several researchers have noted that many examples of behavioural flexibility can be explained by putatively simpler mechanisms (Mikhalevich, Powell, & Logan, 2017). For example, in some cases, behavioural flexibility might be underpinned by a hardwired predisposition or achieved through associative learning (Table 1). Currently, it is difficult to gauge whether behavioural flexibility in cephalopods is underpinned by complex cognition because recent claims are based on anecdotal evidence rather than empirical tests that control for the possibility of simpler explanations (Amodio, 2019; Schnell & Clayton, 2019; Schnell & Vallortigara, 2019). Thus, key questions remain

Table 2. Complex cognitive abilities that are shared across species. A catalogue of animals that share comparable complex cognitive abilities. Among these animals, apes and corvids have been tested most frequently. This catalogue is not exhaustive but represents a subset of studies, and it is important to note that absence of evidence is not evidence of absence

Cognitive ability	Evidence across taxa
Episodic-like memory	Evidence in apes (Martin-Ordas *et al.*, 2010), rodents (Babb & Crystal, 2006; Ferkin *et al.*, 2008), corvids[a] (Clayton & Dickinson, 1998; Zinkivskay, Nazir, & Smulders, 2009), zebrafish (Hamilton *et al.*, 2016), and cuttlefish (Jozet-Alves, Bertin, & Clayton, 2013).
Self-control	Evidence in primates (Beran *et al.*, 1999; Beran, 2002; Evans & Beran, 2007; Anderson, Kuroshima, & Fujita, 2010), canids (Leonardi, Vick, & Dufour, 2012) (reviewed in MacLean *et al.*, 2014), corvids (Dufour *et al.*, 2012; Hillemann *et al.*, 2014) and parrots (Auersperg, Laumer, & Bugnyar, 2013; Koepke, Gray, & Pepperberg, 2015).
Causal and inferential reasoning	Evidence in primates (Call, 2004, 2007; Bräuer *et al.*, 2006; Schmitt & Fischer, 2009; Seed *et al.*, 2009a; Hill, Collier-Baker, & Suddendorf, 2011; Heimbauer, Antworth, & Owren, 2012; Marsh & MacDonald, 2012), elephants (Plotnik *et al.*, 2014), canids (Erdohegyi *et al.*, 2007), corvids (Seed *et al.*, 2006; Smirnova *et al.*, 2015; Jelbert, Taylor, & Gray, 2015) and parrots (Pepperberg *et al.*, 2013).
Future planning	Evidence in apes (Mulcahy & Call, 2006; Osvath & Osvath, 2008; Osvath & Persson, 2013; Bourjade *et al.*, 2014) and corvids (Clayton *et al.*, 2005; Correia, Dickinson, & Clayton, 2007; Raby *et al.*, 2007; Cheke & Clayton, 2012; Kabadayi & Osvath, 2017).
Self-recognition	Evidence using the mirror-mark test in chimpanzees and orangutans (Suarez & Gallup Jr., 1981; de Veer *et al.*, 2003; Anderson & Gallup Jr., 2011), dolphins (Reiss & Marino, 2001) elephants (Plotnik *et al.*, 2006), corvids [Prior, Schwarz, & Güntürkün, 2008; Clary & Kelly, 2016; Buniyaadi, Tahajjul Taufique, & Kumar, 2020; but see Clary *et al.*, 2020 and Soler *et al.*, 2020 for conflicting evidence], and cleaner wrasse (Kohda *et al.*, 2018).
Mental attribution	Evidence in apes (Premack & Woodruff, 1978; Call & Tomasello, 2008; Krupenye *et al.*, 2016) and corvids (Emery & Clayton, 2001; Bugnyar & Kotrschal, 2002; Emery, Dally, & Clayton, 2004; Dally, Emery, & Clayton, 2005; Ostojić *et al.*, 2013, 2014, 2017; Bugnyar, Reber, & Buckner, 2016). However, mental attribution abilities in animals, including humans, remain a contentious idea and are still highly debated (Davies & Stone, 1995; Penn & Povinelli, 2007; Heyes, 2014, 2015).

[a]Corvids also exhibit several other behaviours that could be considered hallmarks of an episodic-like memory system including the ability to produce rich and flexible representations of past events and the ability to prepare for specific events in the future (Jelbert & Clayton, 2017).

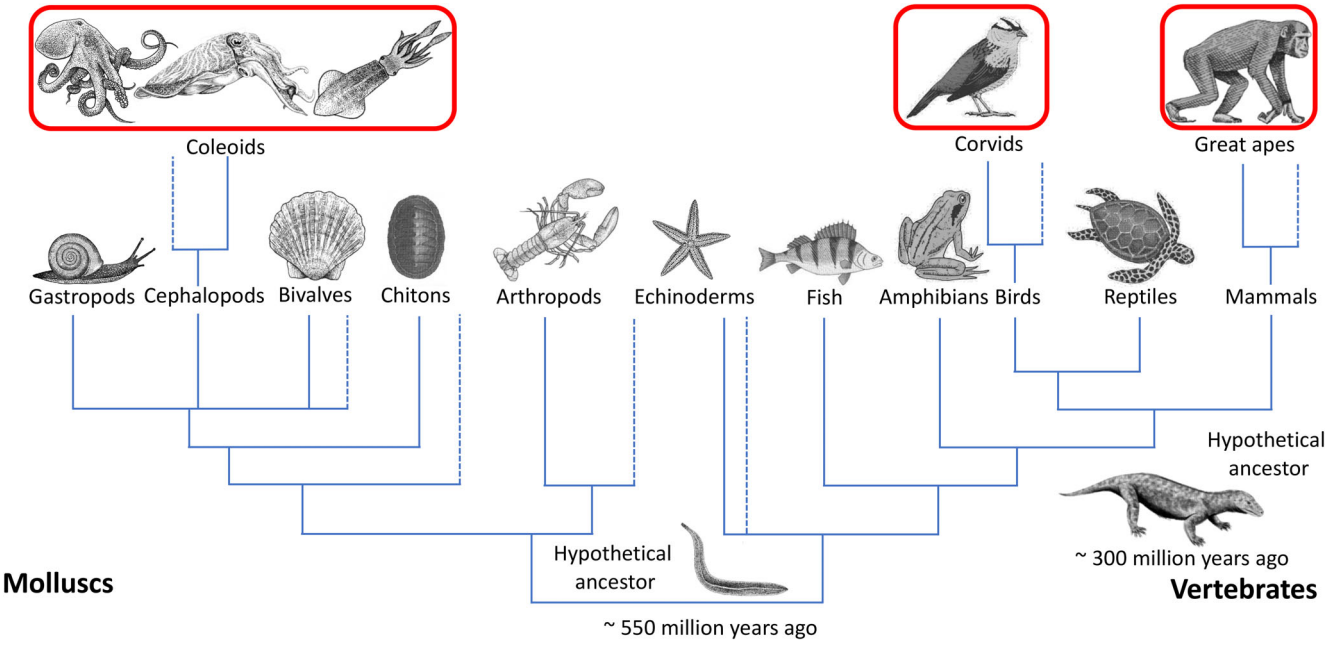

Fig 1. Phylogenetic tree depicting the evolutionary relationship between cephalopods and the more commonly studied vertebrates, corvids, and great apes (image sources: © CCBY-SA: gastropod, echinoderm, chiton, reptile ancestor; © CCBY-NC-ND: cuttlefish; © CCBYSA-NC: worm ancestor; © jenesesimre, stock.adobe.com: octopus, squid, arthropod, bivalve; © artbalitskiy, stock.adobe.com: ape, corvid, fish, amphibian, reptile).

– are cephalopod behaviours underpinned by complex cognition? And, can selective pressures, partially different from those that shaped intelligence in large-brained vertebrates, lead to comparable intelligence in cephalopods? The answers to these questions have far-reaching implications in terms of understanding cognitive evolution as well as how we investigate animal cognition.

To begin to address these questions, we first review the range of cognitive attributes that have been demonstrated in cephalopods. We also present the current reports of behavioural flexibility in cephalopods and provide examples from other animal groups to demonstrate that flexible behaviours might be governed by simple cognitive mechanisms rather than complex cognition. We then refer to comparative cognition literature to outline experimental methods that could help to quantify the cognitive mechanisms that underpin cephalopod behaviours. Finally, we discuss the implications of using cephalopods as non-traditional models for investigating cognitive evolution.

II. CEPHALOPOD COGNITION

Systematic investigations on the anatomy, physiology, and behaviour of cephalopods date back to the mid-19th century (Marini *et al.*, 2017). Since then a wide range of studies has demonstrated that cephalopods possess a highly developed nervous system capable of a range of cognitive processes (Packard, 1972; reviewed in Darmaillacq *et al.*, 2014). Over the last decade, researchers have provided extensive reviews of the cognitive attributes demonstrated by cephalopods (Borrelli & Fiorito, 2008; Amodio & Fiorito, 2013; Darmaillacq *et al.*, 2014; Tricarico *et al.*, 2014; Hanlon & Messenger, 2018). In an effort to avoid redundancy, we will provide a general overview of cephalopod cognition. This is not an exhaustive summary and only represents a sub-set of studies on cephalopod cognition, with a particular focus on the processes that are thought to be prerequisites for more complex cognitive abilities. These will be divided into four categories: sensory perception, perception-based cognition, learning, and memory.

(1) Sensory perception

Cephalopods are renowned for their dynamic behaviours, particularly during camouflage and signalling. Their dynamic lifestyles are often attributed to their large brains and well-developed sense organs (Budelmann, 1994, 1995). They have highly developed visual acuity and are sensitive to polarised light (Shashar, Rutledge, & Cronin, 1996; Shashar, Milbury, & Hanlon, 2002). Although most species have been deemed colour-blind (Brown & Brown, 1958; Marshall & Messenger, 1996; Bellingham, Morris, & Hunt, 1998), they can discriminate between minute changes in contrast (Allen, Michels, & Young, 1985; Chaio & Hanlon, 2001; Mäthger *et al.*, 2006) and are capable of

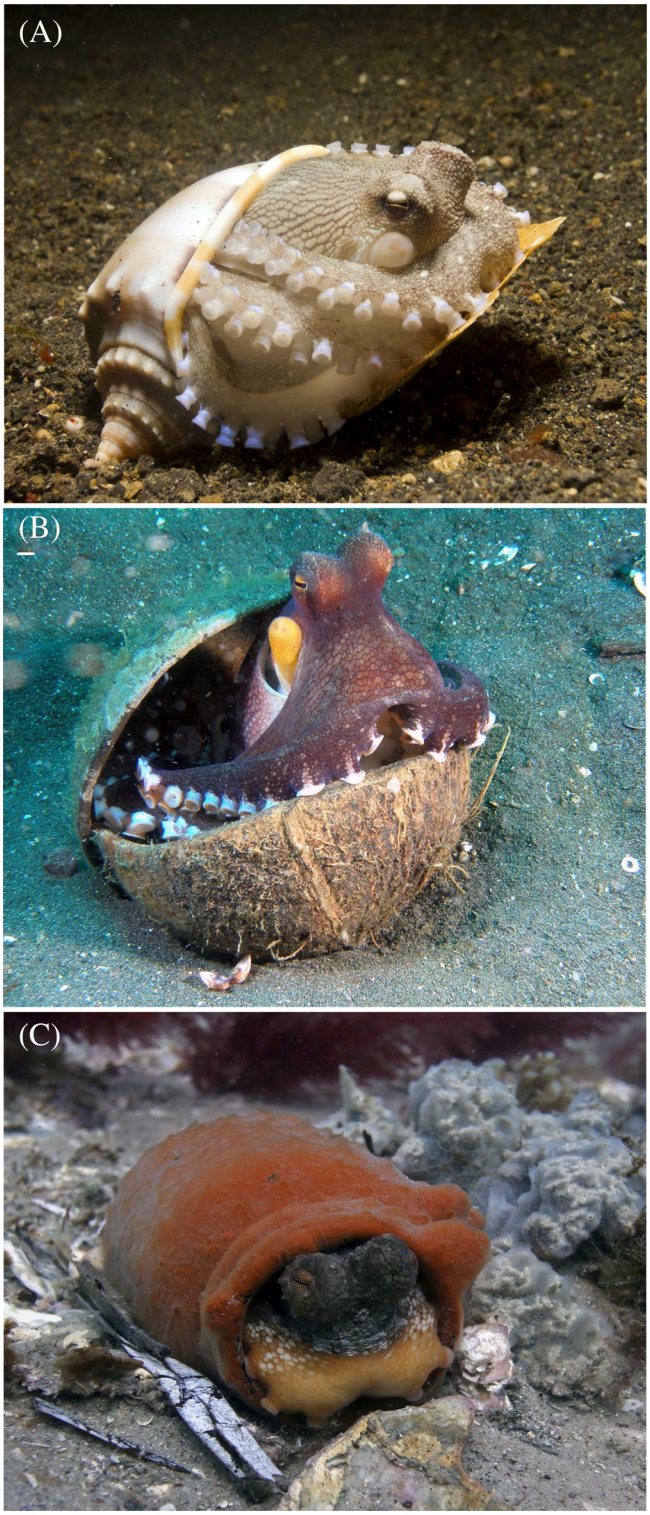

Fig 2. Examples of octopuses using different objects as dens or defensive tools. (A, B) Veined octopus, *Amphioctopus marginatus*, residing in an abandoned conch shell (A; photograph: © davidevison, stock.adobe.com), and encased in two halves of a coconut shell (B; photograph: © Massimo Capodicasa, flickr.com). (C) Sydney common octopus, *Octopus tetricus*, seeking refuge in a glass jar encrusted by a soft sponge (photograph: © Peter Godfrey-Smith).

discriminating between patterns of different size and shape (Sutherland, 1963; Duval, Chichery, & Chichery, 1984; Mäthger *et al.*, 2006). Cephalopods also possess sophisticated chemo-sensory perception. Their suckered arms are equipped with chemoreceptors (Graziadei, 1962, 1964), which facilitate a taste-by-touch ability (Wells, 1963), allowing them to avoid self-entanglement (Nesher *et al.*, 2014) and mediate aggressive and mating behaviours (Cummins *et al.*, 2011).

(2) Perception-based cognition

Other forms of perception that move beyond the processing of sensory stimuli have also been demonstrated in cephalopods. For example, cuttlefish are capable of quantity discrimination, also known as number sense. Specifically, a study on juvenile pharaoh cuttlefish, *Sepia pharaonis*, showed that they were able to discriminate between different groups of prey based on differences in number (Yang & Chiao, 2016). Cuttlefish have also been reported to possess lower forms of object permanence, which is the ability to keep track of objects that can no longer be perceived (i.e. the object has disappeared from sight) (Sanders & Young, 1940). This cognitive process, in conjunction with working memory, is critical for rapid decision-making. For instance, many animals track prey that can hide several times during a single predation pursuit. To make efficient decisions when hunting, an animal must encode and remember the location where the prey was last observed. Object permanence is also thought to be a vital precursor for mental attribution because to understand that objects continue to exist even when they are unseen requires an individual to develop a mental representation of the object (Call & Tomasello, 1999; Gruber *et al.*, 2019).

Another form of perception-based cognition that has been reported in cephalopods includes lower forms of conception formation also known as categorisation. Specifically, two-spot octopuses, *Octopus bimaculoides*, were trained to differentiate between a combination of shells, whereby choosing the odd-shaped shell in the sequence resulted in a food reward. When octopuses were subsequently presented with a new combination of different stimuli that they had not previously observed they were able to transfer learning by choosing the odd stimulus in the new sequence (Boal, 1991). This suggests that octopuses might be capable of inferential reasoning, a process that allows individuals to respond flexibly to a variety of challenges, particularly when faced with new or incomplete information.

(3) Learning

Cephalopods are renowned for their various forms of learning. All cephalopods groups (octopus, cuttlefish, and squid) have a high capacity for learning through association (i.e. action X results in outcome Y). For example, both common cuttlefish, *Sepia officinalis*, and bobtail squid, *Euprymna scolopes*, can learn rapidly to inhibit predatory behaviour through aversive associative learning (Agin *et al.*, 1998, 2006a, 2006b; Zepeda, Veline, & Crook, 2017). Day octopuses, *Octopus cyanea*, can learn to associate a neutral stimulus with a rewarded unconditioned stimulus (i.e. food) through appetitive conditioning (Papini & Bitterman, 1991). Moreover, common cuttlefish can learn to associate a specific prey item with a negative outcome through rapid taste aversion learning (i.e. prey were coated with a quinine-based solution making it bitter) (Darmaillacq *et al.*, 2004).

Cephalopods show a high capacity for discrimination learning and can be taught to make a wide variety of both visual and tactile discriminations (Hvorecny *et al.*, 2007; Borrelli & Fiorito, 2008; Darmaillacq *et al.*, 2014). Cephalopods are also capable of reversal learning, whereby an individual is required first to learn to associate a reward with one of two different stimuli that differ in some visual feature and then subsequently to learn to associate a reward with the alternative stimulus (i.e. discrimination reversal) (Boycott & Young, 1957). Moreover, studies on octopuses, in particular, have revealed that they can perform multiple reversals (Mackintosh, 1964; Mackintosh & Mackintosh, 1963, 1964; but see Bublitz *et al.*, 2017).

Cephalopods also possess advanced spatial learning abilities, including exploratory learning and spatial maze learning (Mather, 1991; Forsythe & Hanlon, 1997; Boal *et al.*, 2000a; Karson, Boal, & Hanlon, 2003; Jozet-Alves, Boal, & Dickel, 2008). For example, two-spot octopuses can use spatial cues to locate shelter in an unfamiliar arena. Most octopuses demonstrated spatial learning in a single day and were able to retain the information over seven days (Boal *et al.*, 2000a). Common cuttlefish locate shelter in a maze by relying on both proximal and distal visual cues, as well as polarised light vectors (reviewed in Jozet-Alves *et al.*, 2008). While, cuttlefish use both vertical and horizontal spatial cues, they show a preference for vertical information over horizontal information (Scatà *et al.*, 2016).

Social learning has been reported in the common octopus, *Octopus vulgaris*, whereby naïve octopuses were able to solve a colour discrimination task by first observing a conspecific demonstrator (Fiorito & Scotto, 1992). By contrast, studies on cuttlefish have reported that learning does not improve by observing conspecifics (Boal, Wittenberg, & Hanlon, 2000b; Huang & Chiao, 2013). It should be noted that the findings from the Fiorito & Scotto (1992) study have not been replicated and this study has since been criticised for lacking controls to determine whether the octopuses were indeed learning through observation or alternative mechanisms (Biederman & Davey, 1993). The findings also led to a debate about the adaptive function of observational learning mechanisms in solitary species, given that they were traditionally assumed to be an adaptive trait of social living. It has since been suggested that alternative mechanisms such as perception, attention, and motivation might facilitate the capacity for social learning (Lefebvre & Giraldeau, 1996; Heyes, 2012). While the capacity for social learning in octopuses is

theoretically plausible, more experiments are needed to test the robustness of the original finding. Perhaps a more suitable candidate for this line of enquiry is the Caribbean reef squid, *Sepioteuthis sepioidea*. These squid are gregarious with typical shoals ranging from 10 to 30 individuals of varying age, providing potential opportunities for individuals to learn from conspecifics through observation (Moynihan & Rodaniche, 1982; Mather, 2010).

The range of different forms of learning demonstrated in cephalopods is impressive but many of these are governed by associative learning mechanisms and need not involve complex cognition. Moreover, similar forms of learning have been reported in diverse taxa that transcend large-brained vertebrates such as insects (reviewed in Giurfa, 2015; Buatois *et al.*, 2018), fish (Kendal *et al.*, 2009; Pike *et al.*, 2010; Brown *et al.*, 2011; White *et al.*, 2017) and reptiles (Paradis & Cabanac, 2004; Noble, Carao, & Whiting, 2012; Kis, Huber, & Wilkinson, 2014).

(4) Memory

There are many studies on cephalopods that demonstrate the extent of memory recall and the effect of memory impairment induced by experimental interference (reviewed in Sanders, 1975; Wells, 1978). Classic studies by Sanders & Young (1940) and Schiller (1949) demonstrate that both octopuses and cuttlefish have short- and long-term memory. Long-term memory has also been reported in squid (Allen *et al.*, 1985; Zepeda *et al.*, 2017). Moreover, in long-term memory studies, the memory trace was reported to last a long time, up to weeks and even months (Boal, 1991; Fiorito & Scotto, 1992).

Many of the traditional studies on memory centre on assessing whether individuals can learn patterns and solve a problem by applying these learnt associations. Such studies often involve multiple training trials and do not test complex forms of memory that transcend learning through association. However, one study has shown that cuttlefish are capable of a complex form of memory that does not solely rely on associative learning but rather on the recollection of a specific event or situation based on what happened, where, and when (Tulving, 1972). Specifically, common cuttlefish can optimise their foraging behaviour using episodic-like memory, by remembering what they had eaten, where they had eaten it, and how long ago (Jozet-Alves *et al.*, 2013). Episodic-like memory (Clayton & Dickinson, 1998) is an important component of mental time travel and is considered to be a precursor for future planning, as it functions as a database to predict future scenarios (Clayton, Bussey, & Dickinson, 2003; Schacter *et al.*, 2012). Current research on cuttlefish shows that they can rapidly adjust their foraging behaviour by integrating information about past experiences as well as proximate-future expectations (i.e. expectations learnt across time). However, whether cuttlefish are capable of future planning – spontaneously planning without relying on learnt patterns – is yet to be tested.

III. BEHAVIOURAL FLEXIBILITY IN CEPHALOPODS

The suite of cognitive attributes exhibited by cephalopods has likely facilitated their remarkable behavioural flexibility, enabling them innovatively to modify their behaviour within various foraging, anti-predatory, and mating contexts (Hanlon & Messenger, 2018; Schnell & Clayton, 2019; Amodio *et al.*, 2019*a*).

(1) Flexible foraging strategies

Similar to apes and corvids, cephalopods exhibit a variety of flexible foraging strategies (Amodio *et al.*, 2019*a*). For example, octopuses avoid visiting the same foraging areas that they depleted of resources (i.e. benthic prey such as bivalves and gastropods) during previous visits (Mather, 1991; Forsythe & Hanlon, 1997). This suggests that octopuses update their memory flexibly to optimise their foraging behaviour. Furthermore, various octopus species use extractive foraging strategies to remove their preferred prey (i.e. crustaceans and bivalves) from its protective armour (Anderson & Mather, 2007). They either pry open the hard encasings using their suckered arms or drill holes through the shell and inject their prey with paralysing toxins (Fiorito & Gherardi, 1999; Blustein & Anderson, 2016). While extractive foraging appears to be confined to octopuses, cuttlefish have developed alternative strategies to optimise their foraging behaviour. A recent study on the foraging behaviour of common cuttlefish demonstrated that they adapt quickly to changes in their environment using previous experience. Specifically, cuttlefish dynamically change their foraging strategies in response to changes in prey availability and proximate-future expectations (Billard, Clayton, & Jozet-Alves, 2020a). Furthermore, mimic octopuses, *Thaumoctopus* sp., have been observed disguising themselves as flounders (Hanlon, Conroy, & Forsythe, 2008; Hanlon, Watson, & Barbosa, 2010) and other species of octopus and cuttlefish have been observed disguising themselves as crawling hermit crabs (Huffard, 2007; Okamoto *et al.*, 2017), which might serve as mimicry to optimise foraging behaviour. Pharaoh cuttlefish, in particular, exhibit this disguise whilst hunting, allegedly to catch more prey (Okamoto *et al.*, 2017).

(2) Flexible anti-predatory strategies

The anti-predatory behaviours of cephalopods are perhaps the most iconic evidence of their behavioural flexibility. While many animals use camouflage to conceal themselves from predators, cephalopod camouflage is unique because they can change the pattern of their skin within milliseconds (Hanlon, 2007). Chromatophore organs in the skin under the direct neuromuscular control of the brain (Messenger, 2001), enable the individual to change its appearance dynamically and rapidly. For example, both cuttlefish and squid can change their body patterns flexibly in response to the perceived threat of approaching fish species that differ in their

predatory strategies (Moynihan & Rodaniche, 1982; Hanlon & Messenger, 1988; Mather, 2010; Staudinger, Hanlon, & Juanes, 2011; Staudinger *et al.*, 2013; Hanlon & McManus, 2020). Some researchers have suggested that squid produce these species-specific responses by perceiving the mental states of the approaching predator, leading to claims of mental attribution (Mather & Ward, 2013; Mather & Dickel, 2017). The same authors suggest that octopuses, cuttlefish, and squid use causal reasoning to select specific skin patterns for particular targets (Mather & Dickel, 2017). However, these claims remain tenuous without conducting experiments to rule out whether these behaviours are underpinned by simpler cognitive mechanisms. Nevertheless, research has recently demonstrated that camouflage in cuttlefish is not simply hardwired, but rather can be shaped by associative learning and individual experience (Hough, Case, & Boal, 2016). These findings suggest that the anti-predatory strategies exhibited by cephalopods involve learning and require decision-making guided by prior experiences.

In addition to camouflage, cephalopods use masquerade to disguise themselves as inanimate objects potentially to evade predation. For instance, some species of octopus and cuttlefish modify both skin patterning, texture, and body posture to disguise themselves as moving algae or a rock (Hanlon, Forsythe, & Joneschild, 1999; Huffard, 2006; Panetta, Buresch, & Hanlon, 2017). The tiny two-toned pygmy squid, *Idiosepius pygmaeus*, use a dorsal adhesive organ to attach themselves to the underside of blades of seagrass (Natsukari, 1970; Norman, 2000), where they float in a head-down position resembling floating algae, seagrass, and flotsam (Moynihan, 1983). Some species of octopus have been observed using defensive mimicry, whereby they mimic inedible, unappetising or venomous animals to deceive predators. Specifically, there have been reports of octopuses disguising themselves as small sponges (Hanlon *et al.*, 2008), flounder (Norman, Finn, & Tregenza, 2001; Hanlon *et al.*, 2008; Hanlon *et al.*, 2010), lionfish, and banded sea snakes (Norman *et al.*, 2001). Caribbean reef squid have also been observed using defensive mimicry, exhibiting body patterns that strikingly resemble parrotfish, *Scarus taeniopterus*, found on the same reef (Moynihan & Rodaniche, 1982).

Other remarkable anti-predatory strategies reported among octopuses include defensive tool-use (Fig. 2). A common octopus was recently featured in the BBC *Blue Planet II* series using its suckered arms to gather and create a protective armour of shells and stones to protect itself from hunting sharks (Jeffs & Brownlow, 2017). Veined octopuses can utilise coconut shells as mobile dens (Finn *et al.*, 2009) (Fig. 2B), and various other species (e.g. *Octopus joubini*, *O. digueti*, *O. tetricus*, *O. vulgaris*) have been observed collecting bivalve and conch shells as well as other objects (e.g. plastic or glass bottles), transporting them, and using them as defensive tools (Ambrose, 1983; Mather, 1994) (Fig. 2).

(3) Flexible mating strategies

Cephalopods also use their ability to change their appearance rapidly to communicate visually with conspecifics (Moynihan, 1985; Lin, Tsai, & Chaio, 2017; Hanlon & Messenger, 2018). Many species produce dynamic displays to convey specific messages and they can use these in a flexible manner. Such flexibility facilitates rapid communication particularly during breeding. For example, male giant Australian cuttlefish, *Sepia apama*, produce multiple displays, performed in succession to convey increasing levels of threat (Schnell *et al.*, 2016). The dynamic nature of cephalopod communication also facilitates flexible mating strategies, which are often dependent on size. For instance, many squid species, including *Sepioteuthis sepioidea*, *Doryteuthis pealei* and *Loligo reynaudii*, vary greatly in size at sexual maturity. Larger males usually produce aggressive displays and defend females vigorously, whereas smaller 'sneaker' males attempt to obtain extra-pair copulations (Moynihan & Rodaniche, 1982; Hanlon, Smale, & Sauer, 1994, 2002; Hanlon, Maxwell, & Shashar, 1997; Shashar & Hanlon, 2013; Naud *et al.*, 2016). Interestingly, small males can switch rapidly between aggressive and sneaker tactics in response to the size of nearby rival males (Hanlon *et al.*, 1997). This demonstrates that the behaviour is facultative, which requires flexible and fast decision-making.

The dynamic communication system of cephalopods also facilitates the rapid production of deceptive signals. For example, at sexual maturity, male giant Australian cuttlefish range between 15 and 60 cm in mantle length. Large and medium-sized males frequently engage in fighting and compete over females using aggressive and defensive behaviours. Small males engage in similar behaviours but if a larger rival male is nearby, they avoid fights through deceptive signalling, whereby they change their appearance both in colour and posture to mimic a female cuttlefish (Norman, Finn, & Tregenza, 1999; Hall & Hanlon, 2002; Hanlon *et al.*, 2005). Some species of cephalopod are able to convey honest and deceptive signals simultaneously. For instance, mourning cuttlefish, *Sepia plangon*, can produce a courtship display towards a female on one side of their body while displaying female patterning on the other side of their body towards a rival male, presumably in an attempt to prevent the rival from interfering with their courtship behaviour (Brown, Garwood, & Williamson, 2012). Sexual mimicry has also been observed in female opalescent squid, *Doryteuthis opalescens*. To deter mating attempts from males, females can mimic the appearance of a male by flashing a white stripe down part of their body, which mimics the approximate size, colour, and position of testes on male squid (DeMartini *et al.*, 2013). Like sexual mimicry in male cuttlefish, this transient behaviour appears to be facultative and only performed by female squid under specific conditions. Transient sexual mimicry in cephalopods has been described as a form of tactical deception (Brown *et al.*, 2012). In primates and corvids, tactical deception is thought to be governed by the ability of an individual to infer that the perspective of a rival might be different from their own (i.e. mental attribution) (Bugnyar & Kotrschal, 2002; Kirkpatrick, 2011). However, whether the same cognitive abilities govern sexual mimicry in cephalopods remains to be tested.

IV. BEHAVIOURAL FLEXIBILITY – EVIDENCE OF COMPLEX COGNITION?

The link between behavioural flexibility and complex cognition has not been systematically or explicitly demonstrated (Mikhalevich *et al.*, 2017). Such a demonstration is particularly important because although flexible behaviours might appear to be sophisticated at a superficial level, an animal might be relying on simple cognitive 'shortcuts' that do not require complex cognitive mechanisms (Mikhalevich *et al.*, 2017). Moreover, sophisticated behavioural phenomena observed in different animals that appear to be similar may be underpinned by different cognitive mechanisms that vary in complexity. For example, over 200 vertebrate species cache food items in different locations and retrieve them at a later date (Vander Wall, 1990; Sutton, Strickland, & Norris, 2016). This is a flexible behaviour because caching and retrieval can be modified in response to different situations. Furthermore, caching is a future-orientated behaviour because the only advantage of caching in the present is the prospect of obtaining food in the future. However, the underlying cognitive mechanisms that drive this behaviour can differ substantially across species. For corvids, caching behaviour involves complex cognitive abilities including episodic-like memory, future planning, and mental attribution. Specifically, California scrub-jays *Aphelocoma californica*, use episodic-like memory to retrieve food discriminately depending on the perishability of the cached item in conjunction with information about what they cached, where, and when (Clayton & Dickinson, 1998). Caching decisions are also based on future-planning abilities in terms of planning what they would like to eat in the future (i.e. caching what they would like to eat for breakfast; Raby *et al.*, 2007), independent of their current motivational state (i.e. food they would like to eat in the present moment; Correia *et al.*, 2007; Cheke & Clayton, 2012). Finally, different corvid species respond to the presence of competitors by re-hiding caches in new places in an effort to reduce theft by pilfering conspecifics, suggesting that they incorporate an attribution of others' knowledge into their caching strategies (Emery & Clayton, 2001; Bugnyar & Kotrschal, 2002; Emery *et al.*, 2004; Dally et al., 2005; Dally, Emery, & Clayton, 2006). By contrast, a study on fox squirrels, *Sciurus niger*, showed that caching behaviour appears to be a hard-wired predisposition, triggered by an environmental cue, such as food availability or the number of social competitors (Preston & Jacobs, 2009). These examples demonstrate how apparently comparable behaviours, in different species, can be driven by different cognitive mechanisms that vary in their degree of complexity. Consequently, when investigating complex cognition, in the absence of empirical tests that control for the possibility of simpler explanations, researchers should take a cautious approach when interpreting cognitive mechanisms that drive behaviours and apply Occam's razor, which states that the simpler explanation for a phenomenon should be favoured over a more complex hypothesis.

V. QUANTIFYING COMPLEX COGNITION: LESSONS FROM COMPARATIVE COGNITION

Distinguishing whether a specific behaviour is underpinned by complex cognition or is solely governed by simpler cognitive mechanisms is challenging, particularly when investigating non-verbal subjects. Fortunately, the field of comparative cognition centres on designing methods based on standardised behavioural criteria that are not dependent on language and thus facilitate the assessment of cognitive abilities in non-verbal animals. Here we consider the use of behavioural criteria as standardised yet adaptable measures of complex cognition.

Pinpointing the underlying cognitive mechanisms that drive behaviours is a stratified procedure involving multiple steps. As a starting point, it is necessary to identify ecologically relevant behaviours that are putatively complex. For instance, many species of corvids cache between 5000 and 11,000 different food items that vary in perishability, store them in different locations and retrieve them at a later date (Chettleburgh, 1952; de Kort & Clayton, 2006). Remembering the location of thousands of caches that vary in perishability and whose degradation rates may vary depending on the substrate in which they are cached, as well as the climate conditions between caching and cache recovery, is likely to have favoured the emergence of sophisticated memory and future-planning abilities (Clayton, Griffiths, & Dickinson, 2000). By linking cognitive abilities to specific socio-ecological challenges experienced in the wild, researchers can begin to develop hypotheses about the evolutionary pressures that contributed to the positive selection of these abilities (Gerlai & Clayton, 1999; Clayton *et al.*, 2000). The next step is to develop behavioural criteria which serve as non-verbal indicators to demonstrate that the animal possesses some aspects of the cognitive ability in question. One of the most noteworthy examples is the development of behavioural criteria to test for episodic-like memory in food-caching jays. Pioneered by Clayton & Dickinson (1998), the researchers presented jays with a caching problem that could only be solved if they could remember the what–where–when components of a specific past caching event. The same behavioural criteria have since been used to demonstrate that distantly related taxa from human children (Russell *et al.*, 2011) and non-human apes (Martin-Ordas *et al.*, 2010) to rodents (Babb & Crystal, 2006) are also capable of solving foraging tasks using episodic-like memory. The final step is to rule out the possibility of alternative explanations for the observed behavioural phenomenon. To achieve this, the design of the experiment needs to be scaffolded with a series of interventionist manipulations that control for predictor variables that might influence the animal's behaviour. Controlling for confounding effects on cognition are best achieved in laboratory environments because field-based studies are typically vulnerable to external influences (Shettleworth, 2010; Janmaat, 2019). Nevertheless, we encourage researchers to complement laboratory-based

studies by also observing and testing animals in the field. A combination of both laboratory and field studies will help circumvent several key issues such as the measurement of fitness benefits in cognition because the adaptive value of a specific cognitive ability will ultimately depend on the environmental context (Cauchoix & Chaine, 2016).

To appreciate the utility of the methods developed in comparative cognition research, we now consider an example pertaining to cephalopod cognition. This example is aimed at investigating whether cuttlefish can optimise their foraging behaviour by planning for the future. In the wild, cuttlefish have long rest periods where they remain stationary and camouflaged (Aitken, O'Dor, & Jackson, 2005). Such periods are punctuated by brief foraging bouts in the open, which require effective foraging strategies. Using methods devised in comparative cognition research, several studies have demonstrated that cuttlefish can optimise their foraging behaviour by using sophisticated memory and future-oriented feeding strategies. Researchers could thus conclude that cuttlefish use episodic-like memory to search for prey discriminately depending on what they had previously eaten, where their previous meal had been sourced and how much time had elapsed since their previous meal (Jozet-Alves *et al.*, 2013).

Such findings were validated in a subsequent study that showed that cuttlefish were able to retrieve specific features of episodic memories, a capacity referred to as source memory. Specifically, cuttlefish were able to adjust their foraging behaviour by retrieving perceptual features that were tied to the source of a previous foraging event, namely whether they had seen the prey item or smelt it (Billard *et al.*, 2020a). Another study found that cuttlefish can adjust their foraging behaviour rapidly in response to changing prey conditions. Cuttlefish were able to learn and remember patterns of food availability to ensure simultaneously that they have enough to eat whilst also prioritising meals to consume more of their preferred prey (Billard *et al.*, 2020b). This dynamic feeding pattern is described as a future-oriented behaviour because the decision-making processes involved are influenced by previous experience and proximate-future expectations. However, at this stage, we cannot validate whether this future-oriented behaviour in cuttlefish is also governed by the ability to plan for the future.

To determine whether cuttlefish can optimise their foraging behaviour by planning for the future, three important abilities involved in future planning need to be quantified. The first is self-control, a vital cognitive skill that underpins future planning because an individual must overcome immediate gratification to fulfil future needs. The second ability is the capacity to anticipate and plan for the future in a novel context, thereby ruling out the possibility that the future-oriented decision-making is based on the application of learnt patterns (Clayton *et al.*, 2003). Finally, the third ability is the capacity to dissociate current and future mental states because to anticipate and plan for future needs an individual must be able to recognise that their future needs might differ from their current desires (i.e. Bischof–Köhler hypothesis; Clayton *et al.*, 2003).

To test for self-control, cuttlefish could be presented with a delayed gratification task similar to the pioneering Stanford Marshmallow test, which was used to test for self-control in children (Mischel, Shoda, & Rodriguez, 1989) and has since been applied to non-human animal models (reviewed in Miller *et al.*, 2019). This test requires an individual to choose between two food items, an immediate but less-preferred food item *versus* a delayed but preferred food item. A key part of the process is to ensure that the individual's decision to wait for the delayed but preferred option truly reflects self-control.

To illustrate this process, consider that some delayed-gratification studies have been criticised for not reliably measuring true self-control due to methodological limitations. For example, many experimental designs do not test whether an individual can sustain continuous inhibition of impulsive responses to the immediate food item (Paglieri *et al.*, 2013). In particular, studies on bees (Cheng *et al.*, 2002), birds (Chelonis *et al.*, 1994; Mazur, 2007) and mammals (Tobin, Chelonis, & Logue, 1993; Tobin *et al.*, 1996; Rosati *et al.*, 2007; Addessi, Paglieri, & Focaroli, 2011) have presented animals with delayed gratification tasks where the choice is irrevocable and thus once the choice is made the individual cannot alter their decision during the trial. This only tests an individual's willingness to attempt to delay gratification but fails to test whether the individual can sustain the inhibition to acquire the better but delayed reward. To overcome this limitation, it is important to allow the subject to discontinue waiting at any point to consume the less-preferred food item, which should remain visible and accessible throughout the trial.

To test for future-planning abilities, cuttlefish could be presented with a 'planning for breakfast' paradigm similar to the experiments conducted on scrub-jays (Raby *et al.*, 2007). This paradigm tested whether the birds could make provisions for a future need when tested in a novel context that eliminated the possibility that their decision was based on previously learnt patterns. Specifically, the birds experienced a hungry room, where breakfast was never provided; and a breakfast room, where breakfast was always provided. Over 6 days, the birds were exposed to each room randomly and during this time food was provided in a middle room, which acted as a corridor between the hungry and breakfast room. The food in the middle room was provided in powdered form, negating any opportunity to carry it away and cache it. Following this exposure, the birds were provided with nuts in the middle room and caching trays were placed in both the hungry and the breakfast room, providing them with the opportunity to cache food in either room. The results showed that the birds cached up to five times more in the trays in the hungry room than the ones in the breakfast room (Raby *et al.*, 2007). A key part of the design of this experiment was to ensure that the subjects were not simply responding to changing conditions by applying learnt patterns, in other words, through associative learning.

Table 3. Comparisons between the vertebrate and the cephalopod brain

	Vertebrate brain	Cephalopod brain
Structure	The hippocampal formation is a major component of the vertebrate brain and is implicated in learning, memory, and spatial navigation (Krebs *et al.*, 1989; Sherry *et al.*, 1989; Doeller, King, & Burgess, 2008; Allen & Fortin, 2013).	Cephalopods have a vertical lobe complex that has been compared to the hippocampus of vertebrates, with similarities in cognitive function, connectivity and neurochemistry (Young, 1971; Nixon & Young, 2003; Shomrat *et al.*, 2015).
Organisation	The vertebrate brain is divided into left and right hemispheres, composed of five lobes and is predominately organised somatotopically (i.e. movements of the body correspond to a specific point in the central nervous system) (Sanes & Schiebert, 2001).	The cephalopod brain does not have obvious left and right hemispheres, is composed of series of ganglia that form 30–40 lobes (Young, 1971; Zullo & Hochner, 2011) and has been suggested to use embodied organisation (i.e. movements are controlled by several parallel overlapping circuits representing individual motor programs) (Hochner, 2012; Levy & Hochner, 2017).
Patterns of connectivity	The hemispheres and lobes are interconnected by commissures, which are highly conserved in the brains of vertebrates (Suárez, Gobius, & Richards, 2014).	The lobes are interconnected by commissures and tracts that create a high degree of crosstalk between the lobes, but the patterns of connectivity are less elaborate than those found in the vertebrate brain (Young, 1971).

To control for this, the birds were unable to cache food items during the exposure period, and thus the option to cache during the novel test period was spontaneous and had not been previously associated with punishment or a reward (Raby *et al.*, 2007).

A similar experiment could be designed for cuttlefish. Instead of caching behaviour as the response variable, the focus could instead be shifted to searching or hunting behaviour. To fulfil the behavioural criteria of anticipating and planning for the future, cuttlefish would be required to preferentially increase searching and hunting behaviour in the hungry room compared to the breakfast room. However, these results alone cannot validate whether cuttlefish can act independently of their current motivational state.

To test whether cuttlefish can dissociate between current and future states, a follow-up study could be conducted using specific satiety to control for the cuttlefish's current state. Specific satiety is achieved by feeding an individual one type of food (e.g. food A) for a period; this usually results in a temporary decline in desire for food A and instead the individual prefers to consume a different type of food (e.g. food B). A similar study was conducted on scrub-jays, whereby the birds were pre-fed one food type (food A) and immediately after this period each subject was allowed to choose between two food items to cache: food A or a different food type (food B) (Correia *et al.*, 2007). Immediately prior to the point of cache recovery, the birds were also offered one of the two food types (food A or B). Results showed that the birds chose to cache the food that they would not have access to in the future regardless of the food type that they had been pre-fed (i.e. were satiated on) (Correia *et al.*, 2007; Cheke & Clayton, 2012). This demonstrated that they could dissociate between their current and future motivational states, and even plan for two alternative future states (Cheke & Clayton, 2012). This example highlights the rigorous measures and interventions that must be implemented to provide substantiated evidence to demonstrate that foraging behaviour in cuttlefish is governed by future planning.

VI. ADVANTAGES OF A CEPHALOPOD MODEL

The current range of model species in comparative cognition literature has made it difficult to uncouple the effects of ecological and social pressures on cognitive evolution since many of the species studied face both challenges. For example, scrub-jays solve the ecological challenge of retrieving previously stored food caches that may or may not degrade by using episodic-like memory (Clayton & Dickinson, 1998). Yet, in the presence of other scrub-jays, they also face the social challenge of outwitting conspecifics to ensure or at least maximise the chance that their caches are not stolen (Clayton *et al.*, 2007). Consequently, predominately investigating social species that face comparable ecological challenges makes it difficult to determine the weight of each effect. Furthermore, the idea that social complexity selects for intelligence has a controversial history as several studies have reported findings inconsistent with the Social Intelligence Hypothesis (Holekamp, 2007; DeCasien, Williams, & Higham, 2017). For example, great apes live in social groups that are comparable in size and complexity to monkey societies, yet only apes exhibit sophistication during cognitive tasks such as learning through imitation and mental attribution (Hare, Call, & Tomasello, 2001; Call & Tomasello, 2008; Krupenye & Call, 2019). In a similar vein, Clark's nutcrackers, *Nucifraga columbiana*, outperform Mexican jays, *Aphelocoma wollweberi*, during spatial memory tasks even though the latter are more social (Kamil, Balda, & Olson, 1994; Olson *et al.*, 1995; Bednekoff *et al.*, 1997). The conflicting evidence generated from these vertebrate comparative studies highlights the need for novel comparisons that extend

current research to diverse species, specifically to species that perform sophisticated behaviours but have been exposed to different forms and/or degrees of ecological and social pressures.

The emergence of intelligence in the animal kingdom has also been attributed to several fundamental characteristics that are shared across apes, corvids, and parrots (Emery, 2006; Seed *et al.*, 2009b; Wirthlin *et al.*, 2018). These include (*i*) a highly omnivorous diet allowing individuals to meet the high energetic demands of maintaining a large brain, (*ii*) a long developmental period allowing them more opportunities to learn essential skills, and (*iii*) extended longevity. However, the influence of each of these characteristics on the evolution of complex cognition cannot be determined by investigating animals that possess all of these features, rather comparative investigations need to be expanded to animal groups with diverse life histories.

Cephalopods are suitable candidates to circumvent some of the current limitations in the literature for several reasons. First, cephalopods perform a wide range of flexible behaviours to meet both ecological and social challenges, many of which have the potential to be underpinned by complex cognitive abilities. Second, cephalopods are widely distributed and are thus exposed to highly variable ecological pressures (Hanlon & Messenger, 2018). They can, therefore, be used to investigate specific ecological factors that select for the evolution of specific cognitive abilities. Third, cephalopods also exhibit varying levels of 'simplified' sociality, defined here as sociality that does not require recognition or cooperation. Within the cephalopods, social organisation ranges from solitary octopuses to aggregating cuttlefish during times of breeding to shoaling squids that school for most of their adult lives (Hanlon & Messenger, 2018; Schnell & Clayton, 2019). An extensive set of phylogenetically controlled comparisons might highlight the effects of low and high levels of social organisation on cognitive evolution.

Using cephalopods as a non-traditional model to investigate cognitive evolution is also likely to provide valuable insights into the key characteristics required to support the emergence of complex cognition because they diverged from the vertebrate lineage over 550 million years ago. The common ancestor of cephalopods and vertebrates was substantially more rudimentary than the common ancestor of birds and mammals and likely resembled a wormlike creature with a simple nervous system (Fig. 1). Consequently, cephalopods deviate drastically from vertebrates and thus exhibit significantly different characteristics from the more commonly studied large-brained vertebrates. Specifically, they have a highly carnivorous diet, a brief developmental period, and reduced longevity. Comparative data between cephalopods and the more traditionally studied vertebrates will thus provide a quantum leap in our understanding of the influences of different characteristics that have facilitated the evolution of intelligent behaviour.

Cephalopods also have significantly different brain structure, organisation, and patterns of connectivity from vertebrates (Table 3) (Young, 1971; Wells, 1978; Budelmann, Schipp, & Boletzky, 1997; Nixon & Young, 2003). These differences are more pronounced than brain divergence between corvids and mammals. However, due to encephalisation of the ganglionic masses (i.e. nerve cell clusters), the cephalopod brain is more similar to the vertebrate brain than to the ganglionic chain of its molluscan relatives (i.e. bivalves and gastropods) (Young, 1971; Hochner, Shomrat, & Fiorito, 2006). Moreover, certain areas of the cephalopod brain show strikingly similar morphological organisation to the vertebrate brain and mediate similar functions (Hochner *et al.*, 2006). For example, the cephalopod cerebral cord, also known as the cerebral ganglion, is analogous to the vertebrate forebrain and midbrain, the cephalopod frontal-vertical lobe is comparable to the vertebrate cerebral cortex and hippocampal formation, and the palliovisceral and pedal cords in the cephalopod brain are comparable to the hindbrain and spinal cord in vertebrates (Young, 1991; Shigeno *et al.*, 2015, 2018).

The vertebrate-like functions of the cephalopod brain, coupled with their behavioural flexibility, make cephalopods a prime non-traditional candidate for investigating the evolution of complex cognition. Moreover, juxtaposing cephalopods with vertebrates, whose cognition has arisen independently through partially different evolutionary pressures, allows us to move beyond the impasses in comparative cognition that have resulted from traditional comparisons among vertebrate species. Comparative evaluations between cephalopods and vertebrates will thus provide a unique opportunity to determine whether certain sophisticated behaviours are underpinned by comparable cognitive sophistication, and by extrapolation, whether such sophistication evolved *via* concurrent processes of divergent brain evolution and convergent cognitive evolution.

VII. CONCLUSIONS

(1) This review provides a general overview of the cognitive attributes of cephalopods, some of which are thought to be vital prerequisites for complex cognition.

(2) We also review the behavioural flexibility exhibited by cephalopods and use examples from other taxa to explain that behavioural flexibility *per se* cannot be used as evidence of complex cognition.

(3) We outline experimental methods from the field of comparative cognition to emphasise the importance of measuring underlying cognitive mechanisms that govern behaviours before labelling them as cognitively complex.

(4) By applying similar experimental designs to investigate cephalopod cognition we can begin to develop a more comprehensive reconstruction of cognitive evolution.

(5) Identifying shared cognitive abilities between cephalopods and distantly related taxa will reveal whether divergent neural architectures can support comparable sophisticated cognition.

(6) At the same time, juxtaposing cephalopods with distantly related taxa will help us understand the degree to which different selective pressures have influenced the emergence of intelligence. If comparable cognitive traits among diverse groups are found, then this will elucidate that intelligence can evolve independently through different evolutionary pathways.

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